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Quantitative analysis of the effect of prey properties on feeding kinematics in two species of lizards

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SUMMARY

Studies of the functional morphology of feeding have typically not included an analysis of the potential for the kinematics of the gape cycle to vary based on the material properties of the prey item being consumed. Variation in prey properties is expected not only to reveal variation in feeding function, but allows testing of the functional role of the phases of the gape cycle. The jaw kinematics of two species of lizards are analyzed when feeding trials are conducted using quantitative control of prey mass, hardness and mobility. For both species, there were statistically significant prey effects on feeding kinematics for all the prey properties evaluated (i.e. prey mass, hardness and mobility). Of these three prey properties, prey mass had a more significant effect on feeding kinematics than prey hardness or mobility. Revealing the impact of varying prey properties on feeding kinematics helps to establish the baseline level of functional variability in the feeding system. Additionally, these data confirm the previously hypothesized functional role of the slow open (SO) phase of the gape cycle as allowing for physical conformation of the tongue to the surface of the food bolus in preparation for further intraoral transport.

Key words: Feeding, lizards, prey properties, functional morphology.

INTRODUCTION

The feeding system in tetrapods has been studied extensively and utilized as a model system to examine key issues in evolutionary biology, including the correlation between organismal design and ecology (Barel et al., 1989; Wainwright and Reilly, 1994; Grant, 1999; Metzger and Herrel, 2005), the role of anatomical novelty in functional specialization and clade diversification (Shubin and Marshall, 2000; Herrel et al., 2001a; Herrel et al., 2001b), and the evolutionary relevance of optimality and functional trade-offs in morphological evolution (Wagner and Schwenk, 2000; Schwenk, 2001). From a life history perspective, the relevance of feeding function is evident, because of its clear link to an individual's fitness (Findley and Black, 1983).

For an individual animal, the kinematic or neuromotor patterns of feeding can be modulated when the animal consumes different types of prey (Bels and Baltus, 1988; Hiiemae et al., 1995; Deban, 1997; Ralston and Wainwright, 1997; Herrel et al., 1999; Sanford, 2001; Schaerlaeken et al., 2008), and specific variations in the properties of the prey such as size, mass, hardness and mobility are expected to have an impact on the function of the feeding system. For example, the consumption of hard prey (durophagy) has been hypothesized to be associated with higher bite force, increased jaw muscle activity, increase in chewing rate and increased length of the slow close phase, and indeed, experimental evidence from a number of studies of a variety of vertebrates has confirmed these predictions (Gans et al., 1985; Hiiemae et al., 1995; Hiiemae et al., 1996; Herrel et al., 1999; Wilga and Motta, 2000; Sanford, 2001; Anderson et al., 2002; Korff and Wainwright, 2004; Herrel and Holanova, 2008). Elucidation of the relationship between prey properties and the kinematics of feeding makes it possible to establish one important aspect of the baseline level of functional variability in the feeding system. It also assists in understanding how the feeding system of a particular species is able to adjust to varying mechanical demands and makes it possible to more accurately compare variability in the feeding system across a broad range of organisms.

The feeding cycle and modulation in response to prey properties in lizards

A good deal of attention has been paid to describing models of generalized terrestrial jaw movement patterns (Hiiemae, 1978; Bramble and Wake, 1985; Reilly and Lauder, 1990; McBrayer and Reilly, 2002), and subsequent analyses of feeding have utilized these models for describing kinematics of the jaws during feeding. In general, these models partition the gape cycle, or opening and closing of the jaws, into four or five discrete and definable phases, with each component having an associated functional role (Fig. 1). Of these kinematic phases, the slow open (SO) phase has previously been hypothesized to be particularly sensitive to sensory feedback and prone to modulation with changes in the properties of the prey (especially mass), because the primary function of the SO phase is to physically conform the tongue to the surface of the food bolus in preparation for further transport (Bramble and Wake, 1985).

The functional role of the phases of the gape cycle and the nature of modulation in feeding can be addressed through studies of the effect of prey characteristics on feeding kinematics. However, to date there have been few studies that quantitatively control the properties of prey during feeding. More typically, studies of this type simply present several types of prey without measuring or controlling the properties of the prey item (but see Hiiemae et al., 1996; Buschang et al., 1997; Bhatka et al., 2004). Previous studies of feeding modulation in lizards have explored the effect of prey properties on feeding kinematics to some degree, and have shown mixed results in terms of establishing a relationship between prey

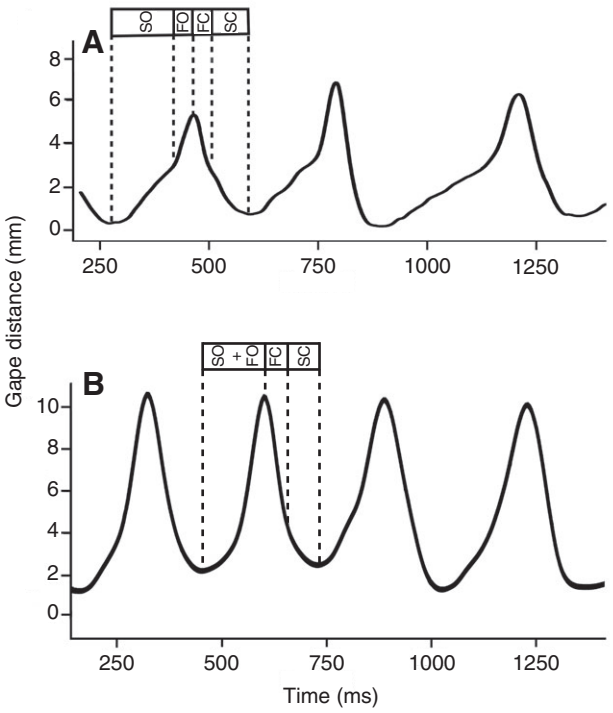

Fig. 1. Typical gape profiles during transport in (A) *Tiliqua* and (B) *Pogona*. Phases of the gape cycle (SO, slow open; FO, fast open; FC, fast close; SC, slow close) are demarcated on one gape cycle for *Tiliqua* and *Pogona*. Note that *Tiliqua* has a slower cycle rate, longer individual cycle duration, and smaller gape distance than *Pogona*. The marked gape cycle in *Pogona* is an example of a cycle where SO and FO phases cannot be easily distinguished from each other.

properties and variation in feeding kinematics (Loop, 1974; Bels and Baltus, 1988; Urbani and Bels, 1995; Herrel et al., 1996; Herrel and De Vree, 1999; Herrel et al., 1999). Especially relevant to the present study, Schaerlaeken et al. (Schaerlaeken et al., 2008) investigated the effect of prey properties on modulation of feeding kinematics in *Pogona vitticeps*, although properties were not individually controlled in order to account for covariation in prey characteristics.

The primary goal of this study was to provide a hypothesis-based analysis of intraoral transport kinematics in two species of lizards when prey properties were explicitly controlled and quantitative data utilized, on the basis of discrete hypotheses. The species examined were chosen not only because of their relative dietary breadth, but also because both make use of lingual intraoral transport (as opposed to inertial intraoral transport), despite drastically different cranial morphologies (e.g. cranial dimensions, tooth morphology, tongue shape and size). Confirmation of the functional hypotheses in this study in two species with differing morphologies and phylogenetic histories provides support for the idea that mechanical prey properties are driving variation in feeding function.

Hypotheses testing related to prey properties

Consumption of prey with increased mass is expected to have specific effects on the kinematics of feeding (Table 1). First, more massive prey is expected to be associated with an increase in the total length of the feeding trial, increase in the length of the intraoral transport stage, and an increase in the number of intraoral transport cycles. These relationships are predicted because the tongue can only transport a food item a specific distance each intraoral transport cycle, and more massive items should theoretically be more difficult to transport. Additionally, because intraoral transport in lizards involves some degree of processing (and intraoral transport and processing are not able to be distinguished from each other in this study), larger food items are expected to require more processing, increasing the magnitude of all of these variables.

Table 1. Hypothesized kinematic predictions related to variation in prey properties

Hypothesis category	Kinematic predictions
Increasing prey mass	Total trial duration increases
Field cricket *vs* locust	Transport stage duration increases
Mealworm *vs* superworm	Number of transport cycles increases
	Absolute SO phase duration increases
	Relative SO phase duration increases
	Gape cycle duration increases
Increasing prey hardness	Total trial duration increases
Cricket *vs* field cricket	Transport stage duration increases
Waxworm *vs* mealworm	Number of transport cycles increases
	Absolute SC phase duration increases
	Relative SC phase duration increases
	Gape cycle duration increases
Increasing prey mobility	Gape distance decreases
Mealworm *vs* mealworm beetle	Number of transport cycles increases
	Absolute FO phase duration decreases
	Relative FO phase duration decreases
	Absolute FC phase duration decreases
	Relative FC phase duration decreases
	Gape cycle duration decreases

The prey items that were compared to test the effect of prey mass, prey hardness and prey mobility are given below each specific hypothesis category in left column.
Phase of the gape cycle: SO, slow open; SC, slow close; FO, fast open; FC, fast close.

Consumption of prey with higher mass should also be associated with an increase in the absolute duration of the SO phase, because of its hypothesized function (see above) (Bramble and Wake, 1985). This has been shown to be the case for tortoises (Bramble and Wake, 1985), an agamid lizard (Herrel et al., 1996) and cats (Thexton et al., 1980), but not in *Pogona vitticeps*, one of the species used in this study (Schaerlaeken et al., 2008). It is also predicted that the duration of the SO phase, as a percentage of the overall gape cycle duration (relative SO duration), should increase, in concurrence with a previous study of variability during feeding in lizards (Herrel et al., 1996). Finally, because of the increased duration of the SO phase, it is predicted that the overall duration of the gape cycle should increase.

Fewer studies have explicitly discussed the effect of prey hardness on intraoral transport kinematics. Herrel et al. (Herrel et al., 1996)

found that in *Agama stellio*, consumption of harder prey [mealworm (hard) *versus* cricket (soft)] was associated with a decrease in gape distance, gape cycle duration and absolute and relative SO phase duration, and an increase in absolute and relative slow close (SC) duration during intraoral transport. A more extensive analysis of prey hardness effects was conducted for two scincid lizards by Herrel et al. (Herrel et al., 1999). Consumption of harder food was correlated with an increase in the number of transport cycles and a decrease in gape distance, although the hard food was a plant material, which also has many other different properties from the soft invertebrate prey than hardness alone. Prey hardness effects have also been observed in *Pogona vitticeps* (Schaerlaeken et al., 2008), primarily relating to an increase in SC duration.

For this study, it is predicted that consumption of hard prey will be associated with an increase in the duration of the feeding trial, duration of the transport stage, and number of transport cycles, as a harder prey should require a longer processing to be reduced properly for swallowing. Additionally, an increase in the absolute duration of the SC phase, and an associated overall increase in gape cycle duration are expected, as this will increase the time that the teeth are applied to the prey. To fully understand the relationship between SC duration and force production for breakdown of hard prey, bite force profiles during feeding on prey of variable hardness are required. However, the predicted increase in SC duration for harder prey is based on the idea that at a given bite force, it will take longer for the teeth to pierce and travel into a harder object (Table 1).

The effect of prey mobility on prey transport kinematics has been examined to a limited degree. Schaerlaeken et al. (Schaerlaeken et al., 2008) reported few effects of mobility on transport kinematics. Herrel et al. (Herrel et al., 1999) found that consumption of mobile prey is associated with a decrease in gape distance, and absolute fast open (FO) and fast close (FC) phase durations, potentially to reduce the chance that a mobile prey will escape from the oral cavity. These findings are also predicted for this study, and additionally, it is hypothesized that gape cycle duration should decrease because of the decreases in FO and FC phase duration, while the number of transport cycles may increase to allow proper immobilization of the prey (Table 1).

The phases of the gape cycle can potentially be varied in two different ways, either by changing the absolute duration of the phase (absolute phase duration) or by changing the duration of a phase measured as a percentage of the overall gape cycle duration (relative phase duration). The primary value in examining variation in both of these variables is the potential to reveal whether the nature of kinematic modulation (absolute or relative durations) may be conserved across clades. For instance, do taxa modulate the length of a specific phase of the gape cycle by changing the length of that phase, thereby changing the length of the gape cycle, or do they conserve the length of the gape cycle and change the relative duration of phases? Comparing the way that the gape cycle is modulated across taxa has implications for our understanding of the conservation of kinematic, and with future inclusion of electromyographic data, neuromotor patterns (Ross et al., 2007).

MATERIALS AND METHODS

Data collection

Kinematic data were collected from five *Pogona vitticeps* Ahl 1926 (Manthey and Schuster, 1999) (Agamidae; bearded dragons; snout–vent length=179±22 mm), three *Tiliqua scincoides* Gray 1825 (Smith, 1937) (Scincidae; blue-tongued skinks; snout–vent length=332±58 mm), and one *Tiliqua rugosa* Gray 1825 (Shea, 1990) (Scincidae; pine-cone skink; snout–vent length=284 mm). All data from the two species of *Tiliqua* were grouped together, as statistical tests revealed that interspecific differences in kinematic variables were no greater than intraspecific differences among the *Tiliqua scincoides* individuals (see Results). *Pogona* and *Tiliqua* are both generalized omnivores that include a variety of plant and animal materials in their natural diet (Kennerson and Cochrane, 1981; Greer, 1989; MacMillen et al., 1989; Dubas and Bull, 1991; Houston, 1998; Hauschild et al., 2000). Similarity in body size (snout–vent length) between all individuals also contributed to choice of species in order to eliminate the potential confounding effects of size on feeding kinematics (Richard and Wainwright, 1995; Wainwright and Shaw, 1999; Hernández, 2000; Meyers et al., 2002; Robinson and Motta, 2002; Van Wassenbergh et al., 2005).

Animals were purchased through commercial dealers and housed in terrariums located at the Laboratory for Functional Morphology in the Department of Biology, University of Antwerp, Belgium. The animal room was kept on a 12 h:12 h light:dark cycle and maintained at an environmental temperature ranging between 25°C and 28°C. When not being used for experiments, animals were fed a variety of food items twice weekly and were provided with water *ad libitum*. Prior to all experiments, the animals were fasted for at least 24 h. All housing, care and experimental procedures were approved by the Institutional Animal Care and Use Committee at Stony Brook University (IACUC #2001-1207) and the University of Antwerp Committee on Medical Ethics (Dossier B01 059). All kinematic experiments were conducted in the room that animals were housed in to minimize disturbances and maintain a constant temperature. A feeding session consisted of multiple, independent trials, during which the animal would usually feed on one, but sometimes multiple food items, which were presented in a random order. Sessions were terminated if the animal was satiated or if kinematic markers came off of the animal. At the termination of a feeding session, all markers were removed and the animal was placed back in its enclosure.

Kinematic data were collected using a six camera, three-dimensional infra-red motion capture system manufactured by Vicon Motion Systems Ltd (Oxford, UK) After camera calibration, the animal being studied was removed from its enclosure, and 4.75 mm retroreflective spherical markers were affixed at eleven locations on the head and neck. A full description and illustration of marker locations are given in Fig. 2. Retroreflective markers placed on the animal subject reflected the infra-red light emitted from the camera strobe back to the camera lenses.

Final reconstruction of marker points using a Vicon workstation PC resulted in a kinematic ‘frame’ with marker points as nodes, making it difficult to definitively distinguish specific feeding behaviors from each other (e.g. prey transport *versus* tongue flicking) based on markers alone. In order to confirm behaviors, a JVC GR-DVL9800 digital camera (JVC Corporation, Wayne, NJ, USA) set to 50 frames s^{-1} was connected to the PC and Vicon Workstation software was used to synchronize the video signal with the Vicon kinematic data.

Experimental software and data processing

Three-dimensional reconstruction of marker locations was performed by the Vicon Workstation software using the direct linear transformation method, which utilizes uniplanar data from multiple cameras within a calibrated space to reconstruct the three-dimensional coordinates of kinematic marker points (Wood and Marshall, 1986; Koff, 1995). Although the raw kinematic data were relatively free of spikes, some smoothing of the data was still desired. A second-order Savitsky–Golay smoothing algorithm (a least

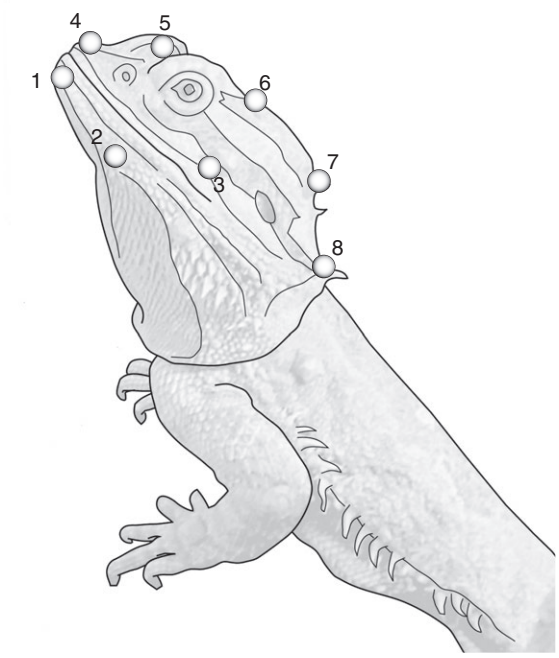

Fig. 2. Diagram of external kinematic marker locations on *Pogona*. The same locations were used for *Tiliqua*. Points include skin directly external to: (1) left anterior lower jaw, (2) left posterior lower jaw, (3) left posterior upper jaw, (4) midline anterior upper jaw, (5) midline midorbital, (6) midline frontal bone, (7) midline posterior parietal bone, (8) midline third cervical vertebra. Marker locations 1–3 were mirrored on the right side of the head.

squares polynomial method that eliminates high frequency noise and preserves low frequency signal) was used. Igor Pro v.4.04 software (WaveMetrics, Lake Oswego, NY, USA) was used for smoothing and for a subsequent Fourier analysis used for confirmation.

To identify the timing of the SO-FO and FC-SC transitions, a custom-written Igor macro (provided by C. Ross, University of Chicago) computed the second derivative of displacement data and identified local minima and maxima that corresponded to changes in jaw opening and closing velocity. This macro always identified a change in the rate of jaw opening/closing velocity, even though in some cases comparison of phase slopes indicated that there was no visual difference between phases (for example between SO and FO). In these cases, opening or closing was grouped into a single SO/FO or FC/SC phase, depending upon the slope of the jaw velocity during that time. These gape cycles were excluded from the present analysis.

Numerous kinematic variables were extracted in order to address the hypotheses described above. These fall into two major categories – variables that can be extracted from *each individual gape cycle* (gape cycle variables) during prey transport only, and variables that *describe overall characteristics of the transport stage or feeding trial.* Gape cycle variables include: (1) maximum gape distance; (2) absolute gape cycle duration; (3) absolute duration of the slow open (SO), fast open (FO), fast close (FC) and slow close (SC) phases; and (4) duration of the SO, FO, FC and SC phases measured as a percentage of the overall individual gape cycle duration (relative duration). Variables describing the overall transport stage or feeding trial include: (1) duration of the entire feeding trial; (2) duration of the transport stage; (3) number of transport cycles; and (4) rate of transport. Other than duration of the feeding trial, only variables extracted from the transport stage of feeding were included in this analysis. The number of cycles analyzed for each individual and prey item are listed in Table 2.

Prey types and properties

In order to evaluate variability and modulation of feeding kinematics, feeding trials for numerous prey types were recorded for both genera. Prey types were chosen based on differences in properties including prey mass, prey hardness and prey mobility, and the ability to avoid covariation when one property was altered.

Invertebrate prey included field crickets (‘field cricket’, *Gryllus campestris*), house crickets (‘cricket’, *Acheta domestica*), king mealworms (‘superworm’, *Zophobas morio*), migratory locusts (‘locust’, *Locusta migratoria*), waxworms (‘waxworm’, *Galleria mellonella*), adult yellow mealworm beetles (‘beetle’, *Tenebrio molitor*) and yellow mealworm larvae (‘mealworm’, *Tenebrio molitor*). The only plant item consumed was apple.

For invertebrate prey, average linear dimensions and mass, prey hardness, and a qualitative assessment of prey mobility were recorded (Tables 3 and 4). Since measuring mass of each individual invertebrate food item was not practical because of the large number of prey items and their movement, at the end of the study a sample of each food type was measured and weighed, and averages calculated. For apple pieces, the mass of each individual food item was recorded prior to feeding.

Hardness of identical food types has been measured on a large sample of invertebrate and plant items by other researchers (Herrel

Table 2. Number of transport cycles analyzed for each individual and food type

		Food type							
Species	Individual	Apple	Beetle	Cricket	Field cricket	Locust	Mealworm	Superworm	Waxworm
Tiliqua	1	145	0	62	127	100	62	76	67
	2	67	126	26	31	109	54	65	69
	3	4	11	18	0	31	11	25	21
	4	0	0	0	0	0	8	34	13
	Total	**216**	**137**	**106**	**158**	**240**	**135**	**200**	**170**
Pogona	1	n.a.*	44	11	55	20	44	49	16
	2	n.a.*	33	61	34	47	31	29	59
	3	n.a.*	79	72	97	0	54	95	62
	4	n.a.*	112	113	114	0	59	84	15
	5	n.a.*	0	77	0	0	5	21	6
	Total	n.a.*	**268**	**334**	**300**	**67**	**193**	**278**	**158**

*n.a., no apple data were collected for *Pogona*.

Table 3. Descriptive statistics for non-variable mass invertebrate prey items

Prey type	*N*	Mass (g)	Length (mm)	Width (mm)	Height (mm)
Beetle	28	0.11±0.03	13.99±0.81	5.07±0.40	3.01±0.19
Cricket	20	0.39±0.10	20.95±1.83	5.61±0.68	5.52±0.47
Field cricket	110	0.46±0.26	24.52±1.84	7.67±1.00	7.30±0.70
Locust	44	1.05±0.79	55.80±2.77	9.80±0.77	10.98±0.67
Mealworm	54	0.23±0.15	23.36±2.40	2.97±0.39	2.71±0.25
Superworm	34	0.64±0.11	39.46±3.84	5.26±0.34	4.60±0.38
Waxworm	50	0.25±0.06	19.91±2.57	4.74±0.50	4.64±0.55

N, the number of prey items measured. Values are means ± s.d.

et al., 1999) (A. Herrel and J. Meyers, unpublished data). In these studies, a Kistler piezoelectric force transducer (model 9203B, Kistler, Switzerland) coupled to a charge amplifier (model 5058A, Kistler, Switzerland) was pushed onto the food item until structural failure of the food item occurred. For invertebrate prey, this procedure was performed on the insect carapace.

Prey mobility was scored as either mobile or immobile. Mealworms were considered immobile, whereas mealworm beetles were considered mobile. As these were the only prey used to test the hypotheses regarding the effect of prey mobility on kinematics, they were the only ones assessed for relative mobility.

Analyses

Prey mass analyses involved two types of comparisons, discrete and continuous. Discrete prey mass analysis was a comparison of feeding kinematics when an animal ate two prey items of different type and mass, but similar hardness and mobility. For this study, two discrete prey mass analyses were conducted, field cricket *vs* locust and mealworm *vs* superworm. Continuous prey mass analysis was only conducted for *Tiliqua*, and involved examination of changes in feeding kinematics when the mass of a single food type (apple) was altered.

For discrete prey mass analyses, specific kinematic predictions were addressed using univariate ANOVAs. For the single continuous prey mass analysis, non-parametric rank correlation analysis (Kendall's tau, τ) was utilized. This correlation statistic is a relatively conservative estimate that is especially useful for small datasets with a large number of tied ranks (Field, 2005), as was the case for this study. Two prey hardness comparisons were performed for each species of lizard, cricket (soft) *vs* field cricket (hard) and waxworm (soft) *vs* mealworm (hard). A single prey mobility comparison between mealworms (immobile) and beetles (mobile) was made. Specific kinematic predictions related to changes in prey hardness and prey mobility were evaluated using univariate ANOVAs. In order to ensure that only one material property was varied at a time, univariate ANOVAs were also performed on prey material properties for all two-item comparisons (e.g. field cricket *vs* cricket, mass comparison).

Kolmogorov–Smirnov goodness of fit tests assessed the data for normality, and Levene's test of homogeneous variances was conducted to determine whether analysis of variance (ANOVA) could be used (Sokal and Rohlf, 1995). If the data were significantly different from normal, nonparametric statistics were used. If variances of data being compared were heterogeneous, timing, linear and angular variables were logarithmically transformed and percentage variables were arcsine transformed (Sokal and Rohlf, 1995). If variances were still heterogeneous, the assumptions of ANOVA are violated, and nonparametric alternatives were used. Because all analyses involved specific kinematic predictions, step-down procedures for multiple comparisons, used to adjust significance levels for univariate ANOVAs (Holm, 1979; Rice, 1989), were not required. All statistical analyses were conducted using SPSS v.11.0 (SPSS Inc., Chicago, IL, USA).

RESULTS

Prey properties and comparisons

Means and standard deviations for mass and linear dimension of invertebrate (non-variable) prey items, including beetles, crickets, field crickets, locusts, mealworms, superworms and waxworm are listed in Table 3. Descriptive statistics for hardness (Herrel et al., 1999) (A. Herrel and J. Meyers, unpublished data) are listed in Table 4.

Univariate ANOVAs were performed on the material properties of the prey used for prey mass and prey hardness comparisons (Table 5). These tests revealed that there were significant differences in prey mass for the field cricket *vs* locust ($P<0.001$) and mealworm *vs* superworm ($P<0.001$) comparisons, but no difference in prey hardness and mobility. For hardness comparisons, there were significant differences in hardness for the cricket *vs* field cricket ($P<0.001$) and waxworm *vs* mealworm ($P<0.001$) comparisons, but no difference in prey mass or mobility. Because mobility was rated on a qualitative scale with mealworms considered relatively immobile and beetles considered mobile, statistical testing was not used to determine differences in prey mobility.

Intrageneric *Tiliqua* analysis

In order to confirm that the two species of *Tiliqua* could be grouped together in subsequent analyses, two-way and univariate ANOVAs were performed. Univariate ANOVAs were conducted for any kinematic variable that showed significant interaction effects in the two-way ANOVAs. *Post-hoc* Tukey's tests performed on the univariate ANOVAs were used in order to determine whether the

Table 4. Mean hardness for non-variable mass invertebrate prey items

Prey type	*N*	Hardness (N)
Apple	25	22.23±6.58
Beetle	14	2.41±0.48
Cricket	36	1.66±0.91
Field cricket	90	2.58±1.52
Locust	25	2.32±2.01
Mealworm	34	2.59±1.07
Superworm	15	3.06±0.70
Waxworm	30	1.12±0.31

Data from Herrel (Herrel et al., 1999) and A. Herrel and J. Meyers, unpublished data.
N, number of prey items measured. Values are means ± s.d.

Table 5. *F*-ratios and significance levels of univariate ANOVAs testing for property differences of prey items used in kinematic comparisons

	Prey mass	Prey hardness	Prey mobility
Mass comparison			
Field cricket *vs* locust	90.970***	2.46	0.00
Mealworm *vs* superworm	147.387***	3.35	0.00
Hardness comparison			
Cricket *vs* field cricket	1.858	12.303***	0.00
Waxworm *vs* mealworm	1.046	66.33***	0.00

Significant difference at *$P<0.05$, **$P<0.01$, ***$P<0.001$.

Table 6. *F*-ratios, significance levels and directionality of differences in kinematic variables for two prey mass comparisons (field cricket *versus* locust and mealworm *versus* superworm) in *Tiliqua* and *Pogona*

	Tiliqua				*Pogona*			
Comparison/Variable	Prey type	Directionality	Prey type	*F*-ratio	Prey type	Directionality	Prey type	*F*-ratio
Field cricket *vs* locust								
Trial duration	Field cricket	<	**Locust**	18.94***	Field cricket	<	**Locust**	17.65***
Transport stage duration	Field cricket	<	**Locust**	22.59***	Field cricket	<	**Locust**	6.50*
Number of transports	Field cricket	<	**Locust**	5.55*	Field cricket	=	Locust	0.343
SO phase duration	Field cricket	<	**Locust**	20.97***	Field cricket	<	**Locust**	301.61***
SO as % of cycle	Field cricket	<	**Locust**	14.95***	Field cricket	<	**Locust**	189.07***
Gape cycle duration	Field cricket	<	**Locust**	138.63***	Field cricket	<	**Locust**	388.83***
Mealworm *vs* superworm								
Trial duration	Mealworm	<	**Superworm**	7.36*	Mealworm	<	**Superworm**	24.46***
Transport stage duration	Mealworm	<	**Superworm**	10.81**	Mealworm	<	**Superworm**	23.84***
Number of transports	Mealworm	<	**Superworm**	10.75**	Mealworm	<	**Superworm**	13.39***
SO phase duration	Mealworm	<	**Superworm**	9.66**	Mealworm	<	**Superworm**	10.91***
SO as % of cycle	Mealworm	=	Superworm	0.02	Mealworm	=	Superworm	2.41
Gape cycle duration	Mealworm	<	**Superworm**	28.47***	Mealworm	<	**Superworm**	30.566***

Bold type indicates the prey item associated with the larger kinematic value. SO, slow open phase of the gape cycle.
Significant difference at *P<0.05, **P<0.01, ***P<0.001.

single *Tiliqua rugosa* was involved in a larger number of significant (P<0.05) pairwise differences than each of the *Tiliqua scincoides* individuals were. This test was conducted for all kinematic variables when feeding on superworms and waxworms, the two prey types for which data from all individuals was available. A larger number of pairwise differences indicates that an individual animal is more distinct from other individuals in terms of its kinematics.

Results indicate that for superworms, the single *Tiliqua rugosa* was different for 7.1% of the possible pairwise comparisons, whereas the two *Tiliqua scincoides* individuals differed in 16.7% and 11.9% of the possible comparisons. For waxworms, the single *Tiliqua rugosa* was different for 35.7% of the possible pairwise comparisons, whereas the three *Tiliqua scincoides* individuals differed in 40.5% and 35.7% of the possible comparisons. Because these results did not indicate that *Tiliqua rugosa* had feeding kinematics that were more distinct from the *Tiliqua scincoides* individuals than the *Tiliqua scincoides* were from each other, all *Tiliqua* individuals were grouped together.

Prey mass analyses

Increasing prey mass while keeping prey hardness and mobility constant was predicted to be associated with increased total trial duration, transport stage duration and number of transport cycles. Additionally, it was hypothesized to be correlated with an increase in absolute/relative duration of the SO phase and gape cycle duration (see above, Table 1).

The first comparison for *Tiliqua* was a discrete mass comparison (see above) between field crickets (average mass=0.46±0.26 g) and locusts (average mass=1.05±0.79 g). All but one of the predictions were confirmed, with total feeding trial duration, transport stage duration, number of transport cycles, absolute and relative SO phase duration, and gape cycle duration, greater when feeding on locusts than on field crickets (Table 6, left column). For the second discrete mass comparison, between mealworms (average mass=0.23±0.15 g) and superworms (average mass=0.64±0.11 g), the results were the same as for the first comparison with the exception of relative SO phase duration, which did not differ between the two prey items (Table 6, left column). The final prey mass analysis was for a continuous increase in mass of apple pieces. A significantly positive correlation was found between increasing mass and increased trial duration, transport duration, number of transports, gape cycle duration, and absolute SO duration, and there was no correlation between mass and relative SO phase duration (Table 7).

Only two discrete mass comparisons, and no continuous mass comparisons, were possible for *Pogona*, and in general the results were the same for both comparisons. When feeding on locusts, trial duration, transport duration, absolute SO duration and gape cycle duration were higher than when feeding on field crickets, and there was no statistically significant difference in the number of transports or the relative duration of the SO phase when feeding on these two prey items (Table 6, right column). For the mealworm–superworm comparison, all predictions but one were met, with feeding on superworms being associated with increased trial duration, transport duration, number of transports, absolute SO duration, and gape cycle duration (Table 6, right column).

Tiliqua and *Pogona* were generally similar in the way that they varied feeding kinematics in response to a change in prey mass. Although no continuous mass comparison was available for *Pogona*, for the two discrete mass comparisons all variables changed in the same direction for both species with the exception of the number of transports in the *Pogona* field cricket–locust comparison, which showed no difference between prey types.

Prey hardness analyses

For both *Tiliqua* and *Pogona*, two comparisons of foods with different hardness but similar mass and mobility were made, the

Table 7. Kendall's tau (τ) correlation coefficient and significance of correlation between prey mass and transport kinematic variables for feeding on apple in *Tiliqua*

Variable	Correlation coefficient (τ)
Trial duration	0.62*
Transport stage duration	0.58**
Number of transports	0.54**
SO duration	0.20**
SO as % of cycle	0.01
Gape cycle duration	0.27**

SO, slow open phase of the gape cycle.
Significant difference at *P<0.05, **P<0.01.

Table 8. *F*-ratios, significance levels and directionality of differences in kinematic variables for two prey hardness comparisons (cricket *versus* field cricket and waxworm *versus* mealworm) in *Tiliqua* and *Pogona*

	Tiliqua				*Pogona*			
Comparison/Variable	Prey	Directionality	Prey type	*F*-ratio	Prey type	Directionality	Prey type	*F*-ratio
Cricket *vs* field cricket								
Trial duration	Cricket	=	Field cricket	1.25	Cricket	=	Field cricket	0.01
Transport stage duration	Cricket	<	**Field cricket**	5.60*	Cricket	=	Field cricket	1.80
Number of transports	Cricket	<	**Field cricket**	9.89**	Cricket	=	Field cricket	2.50
SC phase duration	**Cricket**	>	Field cricket	11.94***	Cricket	<	**Field cricket**	5.52*
SC as % of cycle	**Cricket**	>	Field cricket	5.57*	Cricket	<	**Field cricket**	6.38*
Gape cycle duration	**Cricket**	>	Field cricket	15.91***	Cricket	=	Field cricket	0.01
Waxworm *vs* mealworm	*Tiliqua*		*Pogona*					
Trial duration	Waxworm	=	Mealworm	0.11	Waxworm	=	Mealworm	1.31
Transport stage duration	Waxworm	=	Mealworm	0.07	Waxworm	=	Mealworm	1.48
Number of transports	Waxworm	=	Mealworm	0.008	Waxworm	=	Mealworm	1.71
SC phase duration	Waxworm	=	Mealworm	0.67	Waxworm	=	Mealworm	0.98
SC as % of cycle	Waxworm	=	Mealworm	1.65	Waxworm	=	Mealworm	0.00
Gape cycle duration	**Waxworm**	>	Mealworm	8.89**	Waxworm	=	Mealworm	1.09

Bold type indicates the prey item associated with the larger kinematic value. SC, slow close phase of the gape cycle.
Significant difference at *P<0.05, **P<0.01, ***P<0.001.

first between crickets (average hardness=1.66±0.91 N) and field crickets (average hardness=2.58±1.52 N) and the second between waxworms (average hardness=1.12±0.31 N) and mealworms (average hardness=2.59±1.07 N). Consumption of harder prey was predicted to be associated with increased feeding trial duration, transport stage duration, number of transport cycles, SC phase duration and gape cycle duration (Table 1).

For *Tiliqua*, consumption of field crickets was correlated with an increased duration of transport and number of transports when compared to consumption of crickets, in agreement with the predicted kinematic changes (Table 8, left column). There was no difference in feeding trial duration for the cricket–field cricket comparison, and SC phase duration and gape cycle duration were actually larger in the softer food item. For the second hardness analysis, between waxworms and mealworms, there were no significant kinematic differences in any of the predicted variables except for gape cycle duration, which was larger in the softer food item (waxworms).

For *Pogona*, consumption of harder prey was associated with an increase in absolute and relative SC phase duration in the cricket–field cricket comparison. There were no differences between any other variable for this hardness comparison and no significant kinematic differences for the waxworm–mealworm comparison (Table 8, right column).

There was much less similarity between *Tiliqua* and *Pogona* for prey hardness comparisons than for prey mass comparisons. Whereas *Tiliqua* varied some kinematic parameters for each of the two comparisons, in almost all cases (with the exception of absolute and relative SC phase duration for the cricket–field cricket comparison) *Pogona* did not vary its feeding kinematics in response to changes in prey hardness.

Prey mobility analysis

A single prey mobility comparison was made between mealworms (relatively immobile) and beetles (relatively mobile). Increased prey mobility was predicted to be associated with an increased number of transport cycles, and decreased gape distance, gape cycle duration, and absolute and relative FO and FC durations (Table 1).

In *Tiliqua*, none of these predictions were confirmed, with no difference between any kinematic variables except gape distance and FO duration, which were actually larger in the more mobile prey (Table 9, left column). Relative FO and FC phase duration and gape cycle duration did not differ between the two food types. Values for *Pogona* were more compatible with the predicted direction of kinematic changes. Although there was no statistically significant decrease in gape distance or gape cycle duration, consumption of beetles was associated with a larger number of transport cycles, and

Table 9. *F*-ratios, significance levels, and directionality of differences in kinematic variables for one prey mobility comparison in *Tiliqua* and *Pogona*

	Tiliqua				*Pogona*			
Comparison/Variable	Prey type	Directionality	Prey type	*F*-ratio	Prey type	Directionality	Prey type	*F*-ratio
Mealworm *vs* beetle								
Gape distance	Mealworm	<	**Beetle**	58.41***	Mealworm	=	Beetle	1.57
Number of transports	Mealworm	=	Beetle	2.48	Mealworm	<	**Beetle**	51.77***
FO phase duration	Mealworm	<	**Beetle**	4.72*	Mealworm	<	**Beetle**	13.97***
FO as % of cycle	Mealworm	=	Beetle	1.58	Mealworm	<	**Beetle**	19.68***
FC phase duration	Mealworm	=	Beetle	0.99	Mealworm	<	**Beetle**	15.88***
FC as % of cycle	Mealworm	=	Beetle	0.00	Mealworm	<	**Beetle**	21.51***
Gape cycle duration	Mealworm	=	Beetle	0.71	Mealworm	=	Beetle	1.05

Bold type indicates the prey item associated with the larger kinematic value. FO and FC, fast open and fast close phase of gape cycle, respectively.
Significant difference at *P<0.05, **P<0.01, ***P<0.001.

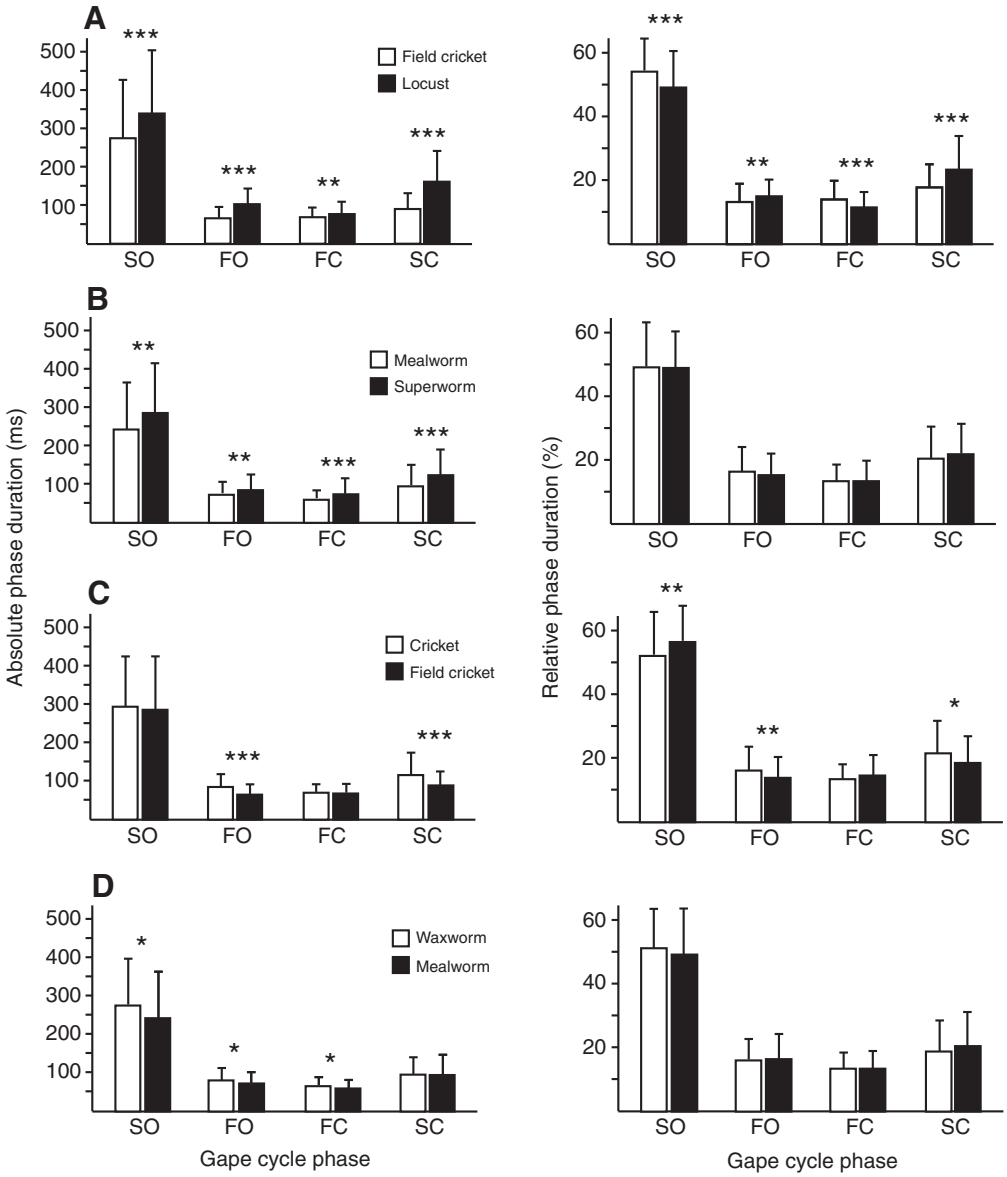

Fig. 3. Absolute (left column) and relative (right column) gape cycle phase durations for all discrete prey property comparisons in *Tiliqua*. In A and B, the less massive prey (field cricket and mealworm, respectively) is indicated by the white bars and the more massive (locust and superworm, respectively) is indicated by the black bars. In C and D the softer prey (cricket and waxworm, respectively) is indicated by the white bars and the harder prey (field cricket and mealworm, respectively) is indicated by the black bars. For all graphs, error bars indicate +1 s.d., and asterisks indicate significant differences between the phase duration for the two prey items (*P<0.05; **P<0.01; ***P<0.001).

larger absolute and relative FO and FC durations than during feeding on mealworms (Table 9, right column).

Nature of gape cycle variation

For both *Tiliqua* and *Pogona*, variation in absolute and relative phase durations was compared for all discrete prey property evaluations (mass: field cricket *vs* locust, mealworm *vs* superworm; hardness: cricket *vs* field cricket, mealworm *vs* waxworm). These comparisons yielded mixed results, depending on the prey property evaluation that was examined. In *Tiliqua*, absolute phase durations (Fig. 3, left column) had a greater tendency to be different between the food types than for comparisons of relative phase durations (Fig. 3, right column). Of the four gape cycle phases for each of the four prey type comparisons, 13 showed difference when absolute phase duration was evaluated, and only seven showed differences when examining relative phase duration. There did not appear to be any trends in terms of which specific phases most often show variation. There were fewer obvious differences between changes in absolute and relative phase duration variance in *Pogona* (9 of 16 showed differences for absolute duration and 10 of 16 showed differences for relative duration; Fig. 4). As for *Tiliqua*, there were no apparent trends regarding which phase varied most often.

DISCUSSION

Prey property effects

For both *Tiliqua* and *Pogona*, there were statistically significant prey effects on feeding kinematics for all the prey properties evaluated (i.e. prey mass, hardness and mobility). Of these three types of prey properties, prey mass had a more significant effect on feeding kinematics than prey hardness or mobility. These results have bearing on the issue of variation of intraoral transport kinematics, and provide information not only regarding whether it exists, but specifically *how* kinematics are varied.

The results of this study indicate that for multiple comparisons in which prey mass is varied but other prey properties are kept constant, kinematics of feeding are generally varied in a manner consistent with the definition of modulation and according to many functional predictions (Table 1). Gape cycle duration is varied and increases with heavier prey. Additionally, both genera vary the absolute duration of the SO phase in association with prey mass, with the directionality predicted by Bramble and Wake

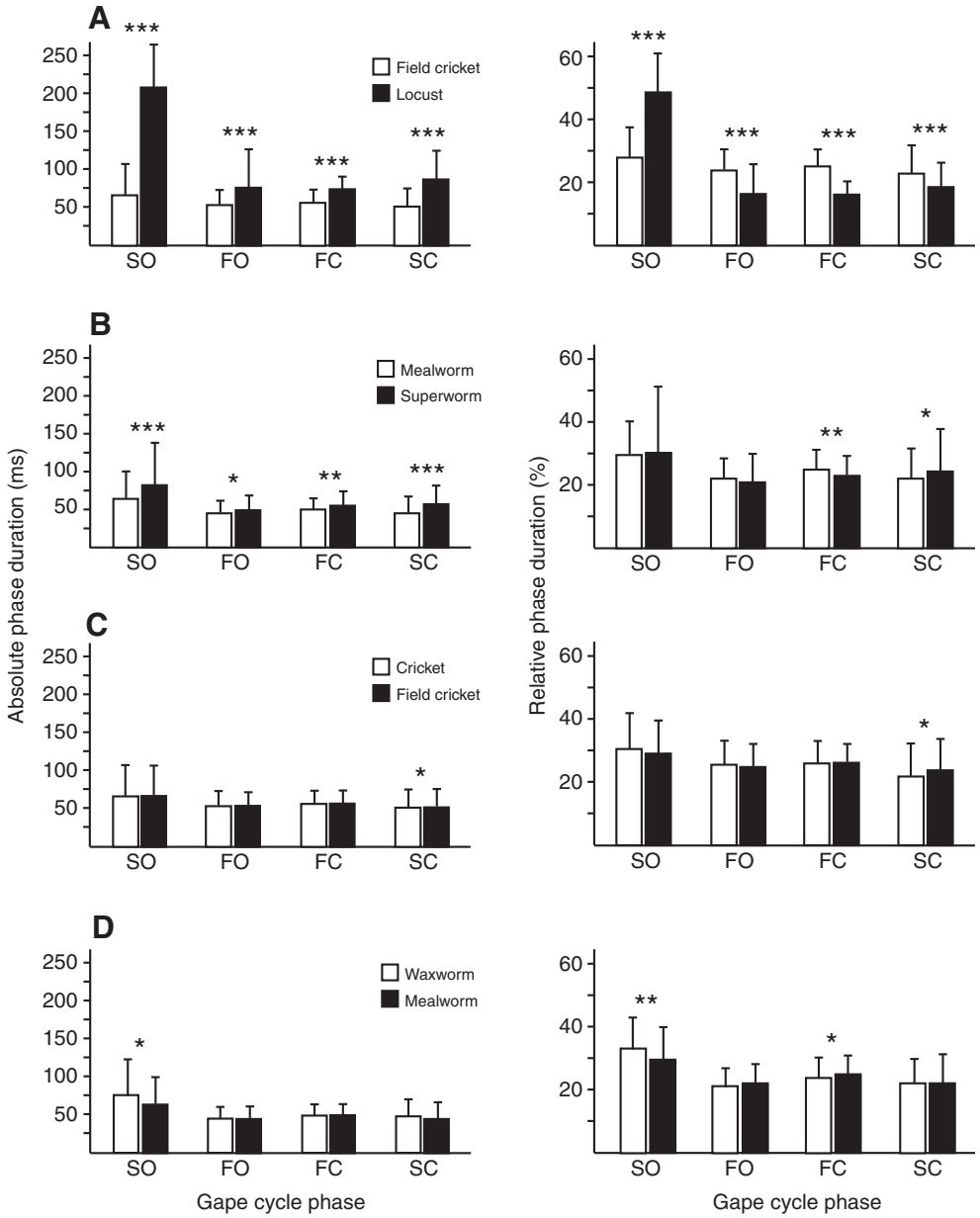

Fig. 4. Absolute (left column) and relative (right column) gape cycle phase durations for all discrete prey property comparisons in *Pogona*. In A and B, the less massive prey (field cricket and mealworm, respectively) is indicated by the white bars and the more massive (locust and superworm, respectively) is indicated by the black bars. In C and D the softer prey (cricket and waxworm, respectively) is indicated by the white bars and the harder prey (field cricket and mealworm, respectively) is indicated by the black bars. For all graphs, error bars indicate +1 s.d., and asterisks indicate significant differences between the phase duration for the two prey items (**P*<0.05; ***P*<0.01; ****P*<0.001).

(Bramble and Wake, 1985). It is interesting to note that although the relative SO phase (i.e. as a proportion of the gape cycle) is modulated for the field cricket–locust comparison, a result that agrees with a previous study of *Agama stellio* (Herrel et al., 1996), relative SO duration is conserved for the mealworm–superworm comparison and the continuous apple analysis of *Tiliqua*. These results indicate that although relative SO duration may be more conserved than absolute SO duration, it can still be varied under certain conditions.

In agreement with other studies that have examined the effect of prey hardness on transport kinematics in lizards (Herrel et al., 1996; Herrel et al., 1999), consumption of harder prey was associated with a decrease in gape cycle duration, at least for *Tiliqua*. However, in contrast to these studies and studies of mammals (Hiiemae et al., 1995; Hiiemae et al., 1996), for most prey comparisons in this study (with the exception of the *Pogona* cricket–field cricket comparison) SC duration did not increase for the harder prey. As a whole, these results indicate that variation in prey hardness has a less significant impact on feeding kinematics in lizards than does variation in prey mass. Although the hardness of the prey items used in these comparisons were significantly different from each other (Table 4), it is possible that if this analysis was expanded to prey that fully exploited the natural dietary diversity of these lizards, the results might differ. As *Tiliqua* is known to consume hard-shelled snails (Gans et al., 1985; Greer, 1989; Hauschild et al., 2000) and *Pogona* routinely eats tough vegetation (Kennerson and Cochrane, 1981; Houston, 1998), inclusion of these items in this study might alter the non-significance of some of the results. Alternatively, it is possible that there was less variation with changing prey hardness than with changing prey mass because variation in prey hardness has a less significant impact on feeding kinematics than does variation in mass. The relevance of prey hardness for the function of the feeding system may be less in these taxa because lizards generally spend less time processing their prey (an action for which prey hardness becomes a major mechanical challenge) and more time transporting it than do many vertebrates. As mentioned above, inclusion of tougher, harder natural prey items in future analyses might help to clarify this issue.

Similarly, both genera generally did not respond to changes in prey mobility in the predicted way or in a manner that agreed with one previous study that had investigated this effect during prey transport (Herrel et al., 1999). Instead of there being a decrease in FO and FC phase duration for mobile prey, these variables were generally unchanged for *Tiliqua* and actually increased for *Pogona*. Additionally, gape distance in *Tiliqua* was greater during transport of the more mobile prey. These results may be explained by the fact that unlike the other prey property comparisons, prey mobility was a qualitative measure and mealworms and beetles differ not only in mobility but also in external dimensions, which may have impacted variability. Although the variation did not match the prediction direction, transport kinematics were still varied, and notably, for *Tiliqua* the relative duration of the FO and FC phases was conserved. However, it is unclear whether this represents active modulation of feeding kinematics or simply variability due to lack of relevance of prey mobility as a factor causing changes in the use of the feeding system during transport.

The examination of the nature of gape cycle variation indicated that in some cases, relative phase durations were conserved when prey with varying properties were consumed, and instead of modulating the relative proportions of each of the gape cycle phases the entire cycle was stretched out, effectively lengthening all phases. However, it should be noted that this was not always the case. For some comparisons relative phase durations were modulated as significantly as absolute durations. Although there is variation in exactly how phases of the gape cycle are modulated, relative durations of phases appear to be more conserved than the absolute durations. However, it is not clear whether this applies to many other lizards or other terrestrial tetrapods as well.

The functional role of the gape cycle phases in lizards

It has been hypothesized that there are functional roles for the various phases of the gape cycle during prey transport in lizards (Bramble and Wake, 1985; Schwenk and Throckmorton, 1989; Kraklau, 1991; Urbani and Bels, 1995; Schwenk, 2000), and the results presented here can address those hypotheses. Most functional hypotheses relating to the phases of the gape cycle in lizards have involved the SO phase, but the FO, FC and SC phases have also been addressed in various studies.

As discussed earlier, Bramble and Wake (Bramble and Wake, 1985) defined the mechanical function of the SO phase during prey transport, and specifically the SO-II phase (the variably present second portion of the SO phase), as conform the tongue to the prey in preparation for effective transport. One potential test of this function is examination of the relationship between SO phase duration and the properties of the prey, and especially prey mass (Bramble and Wake, 1985; Schwenk, 2000). For lingual transport to be effective, prey with larger masses will require a greater bond between the tongue and the prey, which should take a longer duration of time. If the SO phase truly is a preparatory phase for lingual transport, there should be a positive correlation between SO phase duration and mass of the prey that is consumed. This study provides the first explicit evidence, using controlled comparisons, linking the duration of the SO phase to prey mass, lending support to the hypothesis proposed by Bramble and Wake.

Results of this study were less conclusive regarding the function of the SC phase, and the exploration of its function is worthy of future studies, especially considering that this is when physical breakdown of food items occurs. The SC phase is potentially when force transmission from the jaws to the prey occurs, although the degree of force transmission has been debated (Smith, 1984). Although some electromyographic analyses have been undertaken (see Smith, 1982; Gans et al., 1985; Herrel et al., 1997; Herrel et al., 1999) further studies and bone strain studies would be particularly enlightening in understanding the functional role of this phase of the gape cycle.

Comparison with mammalian feeding studies

Several studies have investigated the effect of prey properties on mammalian mastication, generally in primates. Numerous studies have found that when bolus size is experimentally altered, there is a positive relationship with transport cycle duration (Thexton et al., 1980; Miyawaki et al., 2001; Bhatka et al., 2004) and gape distance (Lucas et al., 1986; Van der Bilt et al., 1991; Miyawaki et al., 2001). Studies examining variation based on changes in prey hardness and consistency have been more numerous and have reported somewhat conflicting results. Transport cycle duration has been shown to increase (Anderson et al., 2002) or remain unchanged (Thexton and Hiiemae, 1997) and SC phase duration has a positive relationship with consumption of relatively hard foods (Thexton and Hiiemae, 1997). No studies have investigated whether the duration of the gape cycle phases in mammals is achieved through changes in absolute or relative timing of gape cycle phases, although such information would be interesting in light of the indications from this study that there is greater conservation of relative gape cycle phases than absolute gape phase duration.

Although there are some similarities between lizards and mammals in the way that different aspects of transport kinematics are varied, it is by no means clear that this variation should be interpreted as a behavior that is conserved through evolution. It is just as likely that these phylogenetically disparate groups of organisms are simply responding in similar ways because the mechanical properties of larger or harder food items demand a similar kinematic response in order to be processed and transported adequately. These comparisons are presented simply as a means of demonstrating that establishing whether or not neuromotor patterns during prey transport are conserved through evolution requires that studies be conducted examining similar aspects of modulation and similar kinematic variables in different taxa. Although studies in lizards have focused on variables such as gape cycle and gape cycle phase durations, mammalian studies more typically examine jaw excursions and velocities during mastication. Greater congruence between studies of phylogenetic disparate taxa would be especially useful in addressing hypotheses of kinematic and neuromotor conservation.

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